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COURTSHIP OF THE REDHEAD (APTHYL AMERICANA)

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COURTSHIP OF THE REDHEAD (APTHYA AMERICANA)1

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The annual cycle of the Redhead (Aythya americana) has been studied more intensively than that of most North American ducks. The species winters mainly on the Gulf and east coasts and breeds in the prairie pothole region of the northern United States and southern Canada and in the large marshes of the arid west (Weller, 1964). It nests over water in emergent vegetation and is inclined toward parasitic-laying (Low, 1945; Weller, 1959). Its weight cycle and plumages have been described (Weller, 1957) and related to the chronology of pair formation (Weller, 1965). The present paper integrates my observations with those of previous workers on the courtship displays and pairing activities of the species, presents some quantitative appraisal of the frequency and sequence of displays, and discusses their possible role in the breeding biology of the species.

The earliest reported observations of the courtship of the Redhead scent to have been made by Wetmore (1920: 243-244), but it was Hochbaum (1944: 38-43) who described most of their displays comparatively in his study of the closely related Canvasback (Aythya valisharia). The only more intensive studies of the courtship of a pochard (Aythyini) are those of Lind (1958, 1962) on the Red-crested Pochard (Netta rafina). Recently, McKinney (1965) discussed comfort movements and their use as displays in this and other species, and Johnsgard (1965: 232-234) has described Redhead displays performed on water. General courtship activities of Redheads were outlined by Low (1945) who noted that courtship was prevalent on certain large water areas and occurred mostly in the morning and evening.

The observations reported here were made on breeding grounds at Delta. Manitoba (1952-1954, 1956), and Utah (1955); on wintering areas in Texas (late December and early January, late February and early March, 1960-61) and Chesapeake Bay and Caynga Lake (February and March, 1954); and on the northward migration route in lowa (1961, 1962, 1966) and in Illinois (March, 1957). Observations on some captives of all ages were made at the Delta Waterfowl Station. Work in Manitoba, Utah, and on the east coast was sponsored by the Delta Waterfowl Research Station and the Missouri Cooperative Wildlife Research Unit, Studies in Texas were financed by the American Academy of Arts and Sciences, the Welder Wildlife Foundation, and Iowa State University.

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Figure 1. Kinked-neck Call of the male Redhead. Note the inflated threat, erected crown and neck feathers, and minute pupil.

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Displays

To permit a better analysis of courtship activities, a summary of known displays follows. These descriptions are based on my own observations and photographs but I was aided materially by observations reported by Hochbaum (1944; 18-30) and Johnsgard (1965; 232-234) whose terms were used for aerial displays and displays on water, respectively. Terms used for comfort or intention movements are from McKinney (1965). In the absence of marked birds, the term "pair-male" is used for the individual presumed, because of its behavior, to be the female's mate. Other males are termed "extra" or "lone" males rather than "unmated" males because I have some observations which suggest that paired males may participate in courtship parties when their hens are on the nest.

Rinked-neck Call.—The peculiar, wheezy whee-ough (Wetmore, 1920: 243) or mean call of the male is given with the neck slightly curved and the head feathers erected (Figure 1). The pupils become minute, the bill is opened slightly, and the throat swells. This call occasionally is given by birds resting on land but normally it is restricted to swimming



Figure 2. Head-throw, demonstrating the backwards rocking of the body with the action of laying the crown on the lower back.

birds. In addition to its role in courtship, it is seen regularly when two pairs meet in nesting areas; thus, it may have a threat function. It is also a common response to any disturbance. I noted it especially when I surprised a flock of resting birds or when a large bird landed in a flock of Redheads.

Acrial Countship Note.—When a trio, made up of two males and a female, takes flight, it is not uncommon for the hindmost male to cup his wings downward and call meme as he drops slightly. The delay in flight is brief, and the wing beat is recovered quickly so that the male rapidly catches up with the other birds. Presumably, this is an aerial version of the Kinked-neck Call but 1 do not know whether it is given by the pair-male or the extra male. I suspect it is the former because this display also is seen when only one male accompanies a hen.

Mead-throws—In a courting party (two or more males actively and simultaneously courting a paired or lone female), the males give a spectacular Head-throw similar to that described by Hochbaum (1944: 23) for the Canvasback. This display probably is more extreme in the Redhead than in any other pochard, and may or may not be preceded by a comfort movement such as a Head-flick or Swimming-shake. The intent to give this display usually is signaled when the drake stops swimming with head high. Then, in a somewhat mechanical but rapid movement (stopped only by a shutter speed of 3500 to 3000 second), the head and neck are laid backwards until the crown touches the lower back and the tip of the upper mandible nearly touches the water above



Figure 3. Threat by male with depressed crown feathers,

the almost-submerged rump (Figure 2). The head is brought forward still more rapidly, and the *meone* call is given as in the Kinked-neck Call. I have only once seen this display given by a bird sitting on land. Johnsgard (1965: 234) stated that the head movement was slightly off-center and skewed toward the female.

Turn-the-back-of-the-head,—This display is not highly ritualized in the Redhead, but Johnsgard (1965: 234) reported its occasional occurrence by males responding to Inciting females. He noted that males swimming in front of females move the bill from side-to-side, apparently displaying their somewhat irridescent head plumage.

Threatening and Chasing.—As shown in Figure 3, males threaten either intruding male or aggressive females with their head held low and feathers compressed (sometimes under these circumstances, less intensive threat seems to be indicated by a bird's simply moving directly toward another). I think that low calls are given during this posture because the bills are often slightly open and I have heard the wheezy notes of males given during threats between feeding birds. This head-low posture of the male seems to be that which Johnsgard (1965: 234) termed the Coughing-call in Canvasbacks and reported as rare in Redheads.

When males are challenged by another male or when in pursuit of a female, aggressiveness reaches a stage of direct attack, with head low and bill open (Figure 4).

Females often threaten in a similar fashion but seem to hold their heads higher than do males. Females give a low, typically gutteral



Figure 4 Palradiakes chasing an extra male.



Figure 5. Two courtship parties of Redicads. In the foreground, the fer ale threatens an extra male while her pair-drake calls quietly at her side.

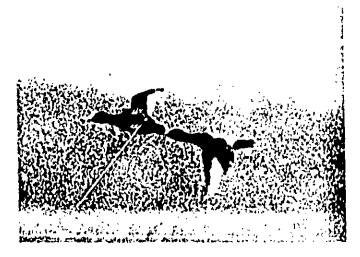


Figure 6. Aerial Tail-pull by drake of part.

call with the bill open (Figure 5). Their aggressive chases are similar to those of males and are even more common and intense.

Underwater Chase and Aerial Chase,—During intense courtship, females attempt to escape from a party of courting males by diving. This is a sudden splash-dive in which the pair-drake and extra males usually participate. Such diving by the hen does seem effective in misleading or discouraging some extra males. The pair-male seems to remain close to the hen underwater but, If lost, scurries to her side as she comes up. In one case, a pair-drake overely swam above the female watching her movements underwater so that he was always by her side when she surfaced. Extra males that were diving were less successful. Extra males come up at various places and skitter toward the female which may respond by another dive or by taking flight. The latter results in an Aerial Chase in which the female is pursued by most males and during which some males drop out and others may join. McKinney (1961) considered aerial and diving chases homologous and indicated that they were prevalent in the early pre-nesting phase of the reproductive cycle. Underwater pursuits are more common among diving ducks than among dabblets, the latter taking flight more readily and engaging in long and erratic courtship flights,

Aerial Tail-pull.—Males of pairs (or occasionally trios) in flight sometimes attempt to pull the female's tail (Hochbaum, 1944). This chase usually does not last long and the female veers to avoid it. Occasionally, males are successful and grip the tail momentarily (see Figure 6). The



Figure 7. Inciting of female Redhead, Palradroke is at right. The fone drake at the left is finishing a Head-throw.

motivation or function of this act is not known. It occurs mostly with isolated pairs during the pre-laying and laying period in May, but I observed it as late as mid-July in Manitoba. I have seen it only once during the spring migration season in central lowa but I did not see it on the wintering areas in Texas. Although this display commonly is seen when pairs are flushed by man, I have observed it on three or four occasions while hidden in a blind so that it does occur in the absence of human disturbance.

Inciting.—With the exception of the aggressive role the female plays in threatening and chasing courting males, her only conspicuous display is Inciting. This is a bill and head movement which, as Johnsgard (1965) pointed out, has a strong Chin-lifting element. It also resembles the threat posture. The bill is lowered toward the side of the neck or side, then quickly raised (Figure 7). This may be repeated many times, Johnsgard (1965) reported that a soft err call was given during the Inciting movement.

Mutual Neck-stretch.—Following encounters with courting males, females rejoin their pair-males and the pair Neck-stretches while facing each other or while at right angles to one another, often with their breasts touching (Figure 8). During this display, the feathers of the male's throat and upper neck are erected. This display lasts only a few seconds, and two birds swim away together.



Figure 8. Mutual Neck-stretch of pair following a conflict with extra males,

Copulation.—Three copulations were observed from beginning to end and parts of this behavior were observed numerous times during this study. Precopulatory behavior is not conspicuous but usually involves Pseudodrinking (Bill-dipping) by the male or by the pair (Figure 9) and

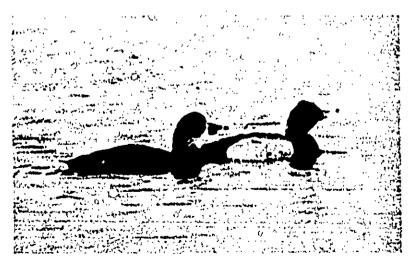


Figure 9. Pseudo-drinking or Bill-dipping.



Figure 10. Bill-down Post-copulatory Posture (photo by Paul Johnsgard),

preening of the back or scapulars (Preen-dorsally of McKinney, 1965) by both sexes. Copulation occurs in the normal anatid manner with the male grasping the female's nape with his bill. Copulation is brief and is followed by a Bill-down Post-copulatory Posture, at least by the male and often by both sexes (Figure 10). In this posture the neck is stretched, and the back of the head is raised as high as possible while the bill nearly touches the front of the neck. Both birds usually swint a short distance in the Bill-down Posture, then preen and bathe. I did not observe the Kinked-neck Call as a post-copulatory behavior as did Johnsgard (1965; 234).

Comfort movements.—Comfort movements such as the Head-flick and the Swimming-shake were observed between or following courtship displays. My data do not permit any definite conclusions as to whether these movements have some signal function in display, whether they are just the normal movements of an active bird, or whether they are an expression of conflict of motivation. Because these movements do not differ significantly in form among species, their descriptions given by McKinney (1965) are satisfactory.

QUARTITATIVE SUMMARY OF DISPLAYS

General observations made during this study clearly demonstrated that certain displays were restricted to certain situations. In the most active

TABLE 1 Occurrence of Some Major Displays and Activities in 61 Courtship Parties Involving a Pair and One or Morg. Extra Males (Total 161 Extra Males)

Item	Average number per party
Extra majes with "pair"	1.90
Chases of extra males by hen	0.80
Chases of extra males by pair-drake	0.17
Chases of pair-drake by hen	0.26
Kinked-neck Cally by pair-drake	1,34
Kinked-neck Calls per individual by extra drakes	0.66
Head-throws by pair-drake	0.29
Head-throws per individual by extra drakes	0.92
Comfort movements by hen	0.19
Comfort movements by pair-drake	0.49
Comfort movements per individual by extra drak	

courtship parties which engaged in threatening, chasing, diving, and flying, few displays were seen. In the less intense and more common courtship parties, the Kinked-neck Call and Head-throw were regular components.

To evaluate these impressions better, records were summarized on the displays of 61 courtship parties. In some cases, several parties involving the same pair were recorded, but party encounters were considered separate whenever the pair was left together after a series of displays with extra males. The summary of data recorded during this study (Table 1) indicates that hens are more active than pair-drakes in chasing intruding males (0.80 to 0.17 chases per party), that Kinked-neck Calls are more commonly given by pair-males than by extra males (1.34 to 0.66), and that more Head-throws are given by unmated than mated males (0.92 to 0.29). Student's t-tests were used to evaluate the significance of these diff rences; all proved significant at the P < .01 level. Because records of the behavior of each extra male in a party were not available, it was necessary to estimate variance of the activity of each extra male by considering the deviations of the mean for all birds in a party from the mean for all individuals in all parties.

The occurrence of certain comfort movements was common among drakes, but these could not be recorded accurately because or the number of birds involved. Thus, they were not tested statistically. Most common were Bill-cleaning (a side-to-side bill-shake). Head-flicks, and Swimming-shakes. Occasionally, preening and Wing-flapping occurred.

CHRONOLOGY AND SEQUENCE OF DISPLAYS

The pair-formation period begins in late December and early January on the Texas wintering areas (Weller, 1965). Only a small percentage

of birds are involved at first and this increases throughout the wintering period. One behavior seen on wintering areas that was not evident on migration or breeding areas was the tendency of females to follow males, Males appeared to be leading the female. The "following action" by the female apparently indicated a willingness to pair. Marked birds were not available to determine whether such "pairs" remain intact during the long spring migration. Presumably, these females were in the early stages of sexual activity, and such females became involved in courting parties. In these cases, males often defended the females which followed them and, at times, they followed the female. Other females were distributed without special reference to males: two or three females commonly were seen together.

During late winter on wintering areas, and later on migration or breeding areas, males normally followed the females, even awaiting their decision to fly. Such males rarely chased or displayed toward their mates. Most displays observed were associated with the conflict situation of the presence of extra males, and with courtship parties formed whenever a female and her accompanying male were met by a sexually active, lone male. The approaching mase usually gave the Kinked-neck Call. The "pair-male" also called and often moved between the female and the intruder. Other males also were attracted, and groups of four to seven males were seen commonly with one female, forming courtship parties (Figure 5). Such parties were conspicuous, even in a large flock, by their tight grouping, their alert posture, and their synchronized movements. The aggressiveness of the pair-male was most evident during highly intense courtship when he chased extra males; at other times he merely maintained a position near his female. Battles between extra males usually were more intense than conflicts between pair-drakes and extra drakes. Both members of the pair kept their heads high (as may aggressive males) when they did take a position opposing the group of extra males. In such situations, the pair may assume a Mutual Neck-stretch.

The female sometimes gave the Inciting posture when approached by extra drakes, directing her movement toward her favored pair-drake and away from the intruding males.

As with many pochards, the female Redhead avoided the attentions of the intruding males by her aggressiveness. Females became extremely aggressive and were responsible for most pair-defense (Table 1). Hens threatened and chased extra males, especially when the latter called, and they often pecked fleeing males viciously. Although when many males were present the female was clearly being harassed, rape was not observed and has not been reported in this species. It was reported in Red-crested Pochards by Lind (1962) but apparently it is not as common

in this tribe as in the Anatini. In active encounters between a pair and extra males, the ben chased one after another of the courting males; occasionally she turned on her own favored male to peck him (Table 1), but he soon was allowed to return to her side. Rebuffed extra males often dropped to the rear of the group and gave a Head-throw; pair-males also gave Head-throws but did so much less commonly (Table 1).

These courtship parties were led by the rapidly swimming female with the favored male nearby. After several rebuffs, extra males usually departed. However, at the height of the courtship period on wintering, migration, and nesting areas, females dived repeatedly to avoid the males, and if still pressed, took flight. The males followed and all rose in a fast-moving, irregular flight which often returned to the same point. Males occasionally left these aerial chases to join other parties or a flock. Other males joined these chases, and up to 14 males were observed following one female.

During migration in April and May, and during May and June on the breeding areas, the following several displays were seen which were not observed on the wintering areas. During migration, aerial chases were common although aerial displays were rare—Aerial Courtship Notes and Aerial Tail-pulls were seen only occasionally while both were common on breeding areas. Copulation was observed on both migration and breeding areas but was not seen during the late winter.

Many birds were "paired" during migration and all females had pairmales on arrival on breeding areas (Weller, 1965). However, courtship parties were common with eatra males courting paired females. In the large Delta Marsh in-southern Manitoba, courtship activity was at its peak when migrants were still moving through breeding areas; large groups of ducks gathered on large pools. Gradually, pairs became distributed over the marsh, using smaller pools of water, and encounters between pairs seemed uncommon and caused little apparent aggressive behavior. Presumably, this is territory establishment by avoidance as noted in Ring-necked Ducks (Aythya collaris) by Mendall (1958: 59-60). During this period the Aerial Tail Pull, the Aerial Courtship Note, and the constant barsh kurr-r-r call given by females became conspicuous and birds engaged mainly in mutual pair-displays. Hochbaum (1944: 27) used the term "nuptial courtship" to describe the behavior of established pairs and noted that copulation occurs only in isolated places after pair bonds are well established. Observations by Low (1945) and those of the present study are in agreement with those of Hochbaum (1944; -30) that conulation was never a product of social courtship and never was more than one male involved.

Discussion

Courtship in pair formation.—The role of courtship in pair formation of ducks has been much discussed, and recent summaries have been made by McKinney (1965) and von de Wall (1965). The pairing process in ducks often is a long one, as noted in Mallards (Anas platyrhynchos) (Weldmann, 1956), and may involve temporary associations before the final mate is selected.

My observations in Texas + females following males (which 1 did not observe on breeding areas) suggests that attachment or at least recognition between two individuals of opposite sexes may occur in the absence of displays. Presumably, the recognition and at least temporary acceptance of a mate aids the female in avoiding other males because the "mate" does some chasing (Table 1) and his presence may be a psychological deterrent to other males. Once 1 placed a flightless captive hen Redhead in the Delta Waterfowl Research Station pond where many wild Redheads visited. She was courted intensively by several males and accepted a wild male as a mate within eight minutes. The other males gradually left the newly formed pair loafing together.

The fact that the female does not always try to leave these social courtship parties indicates a sexual or social interest in the males involved. In fact, observations by other workers suggest that females may encourage the formation of courtship trities by attracting males. Both Hochbaum (1944: 25-32) and Wetmore (1920: 243) described situations in which female Canvasbacks and Redheads, respectively, "entired" males with a head-high posture.

Because females in apparently well established pairs are courted constantly by unmated males, it would appear that such courtship constantly tests and perhaps strengthens the pair bond. According to Weldmann's (1956) observations on Mallards, mates commonly are exchanged until a stable pair bond is established between two individuals. This would seem advantageous to the species because the more aggressive and colorful males presumably would be at an advantage. A choice of males by females is possible because of the excess of males in Redhead as well as many other duck populations (Bellrose *et al.*, 1961).

Origin of some displays.—The origin and motivation of the more complex displays of the Redhead male cannot easily be resolved but several observations may yield evidence regarding these topics. Especially striking is the Head-throw which also is common to many other pochards (Johnsgard, 1965). This posture does not seem to be intentionally directed toward the female or the courting party as a whole, although occasionally the female turns as the following male displays. In fact, the Head-throw

usually occurs after the peak of activity of a courtship party and takes place behind the major group.

The Head-throw has been reported in old female Redheads (Johnsgard, 1965; 232) and Canvasbacks (Hochbaum, 1944; 24). Both Mochbaum (1944; 21) and I have seen it in young Redheads 7½-12 weeks of age, and Dr. William H. Elder (pers. comm.) and Phillips and McKinney (1962) induced it in downy young by treatment with testosterone.

A clue to its origin may be found in the following observation. When attempting to capture a marked brood of Redheads in the Minnedosa pothole region of southern Manitoba, Alex Dzubin and I observed the female leave the brood in cover and go to open water. She was one of the most broody females we had ever observed, and her excitement was expressed in constant, loud calling and in a continuous pre-flight Chin-lifting. The Chin-lifting gradually became more and more extreme and eventually became a full Head-throw which was slightly off-center. The Head-throw was given several times.

In this regard, it is highly significant that the Head-throw usually is given by males in a post-hostile situation and that, on windy days, males stop and may turn up-wind before giving the display. Often, they then rejoin the courting party. It seems possible that this is a highly ritualized Chin-lifting posture given in a situation of conflict between sexual and flight tendencies. Moreover, it may involve elements of preening or ofling because of the off-center rolling movement of the head.

Courtship in species isolation.—The similarity of the displays and general courtship activities of Redheads and Canvasbacks is striking and further points out that these are species of fairly recent separation. However, according to Gray (1958), no wild hybrids of Redheads and Canvasbacks have been reported although hybrids are common in captivity (Hochbaum, 1944; 38). Wild hybrids would be difficult to identify but can be expected on the basis of several observations of interspecific courtship. Hochbaum (1944; 40) reported seeing a Redhead drake actively participating in a Caavasback courtship party and Timken (1967) observed a Canvasback drake participating in a Redhead courting party in the wild. In Manitoba, I once saw a male Redhead with a female Canvasback in the wild, and they behaved as a pair.

There are many characteristics that may function in species recognition and thus isolation between Redheads and Canvasbacks. The following possibilities need to be tested in Redheads and Canvasback, respectively: forchead shape (rounded versus elongate), head color (reddish versus blackish-red), body color (gray versus white), bill color during the breeding season (bluish versus black), different call notes, and the form and duration of the Head-thray (extreme and fast versus short and slow).

SUMMARY

The displays of the Redhead are described and illustrated. Major displays of the male are the Kinked-neck Call and the Head-throw. Females are highly aggressive and maintain a position near a preferred male. Courtship occurs on wintering, migration, and nesting areas and, when directed towards a paired female, forms a constant test of the pair bond. Intensive courtship may incorporate diving and aerial chases resulting from the female's efforts to escape pursuing males.

A quantitative summary of 61 courtship parties suggests that hens are more inclined to chase extra drakes than are pair-drakes, that pair-drakes give more Kinked-neck Calls than do extra drakes, and that extra males give more Head-throws than do pair-males.

The courtship of the Redhead is very similar to that of the Canvasback but no hybridization has been reported in wild populations. Experimental studies of isolating mechanisms need study.

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